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by

Philip Unitt, Karen Messer, and Marc Théry

No. 31
31 May 1996
Proceedings of the
San Diego Society of Natural History

ISSN 1059-8707

PROCEEDINGS

of the

San Diego Society of Natural History

Founded 1874

Number 31 31 May 1996

JUL 29 1996
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Taxonomy of the Marsh Wren in Southern California

Philip Unitt

San Diego Natural History Museum, P. O. Box 1390, San Diego, California 92112

Karen Messer

Department of Mathematics, California State University, Fullerton, California 92634

Marc Théry

Centre Nationale de la Recherche Scientifique, URA 1183, Muséum National d'Histoire Naturelle, Laboratoire d'Ecologie Générale, 4 Avenue du Petit Château, 91800 Brunoy, France

ABSTRACT.—At least three subspecies of the Marsh Wren (*Cistothorus palustris*) occur in southern California. *C. p. plesius/pulverius* is a widespread migrant and winter visitor and breeds in the Owens Valley south to Owens Lake. It is characterized by large size, pale tawny rump and scapulars, a nearly white breast, mostly brown crown, and bold white back streaks. It arrives in its winter range mainly in mid to late September and departs mainly in April. A distinction between *plesius* and *pulverius* seems likely but was not examined in this study. *C. p. aestuarinus* is resident from the Colorado River and Imperial Valley northwest locally through the Mojave Desert, and along the coast from Ventura County north through northern California to southwestern Oregon. It is characterized by its medium size, moderately dark rufous rump and scapulars, a crown partly black and partly brown, and narrow to moderate white back streaks. Its breast ranges from moderately buff (usually in the Colorado Desert; frequently in the Mojave Desert and along the coast) to deep buff or brown (usually in the Sacramento Delta; frequently in the Mojave Desert and along the coast). A distinction between *aestuarinus* and *deserticola* could be maintained if specimens from the type localities only (Sacramento Delta and Imperial Valley, respectively) were considered, but the area of intergradation is so large (Mojave Desert; coastal central and northern California) that the distinction does not seem broadly useful.

The resident population of coastal southern California (Los Angeles to San Diego counties) is differentiated by its small size, largely black crown, and deep rufous rump and scapulars. At least 94% of specimens of this population can be distinguished from all other Marsh Wren subspecies, so we propose it be known by the new name *Cistothorus palustris clarkae*.

No California Marsh Wren population agrees with that of southwestern Washington, with its largely dark brown crown, broad brown nape collar, and consistently narrow whitish streaks on a reduced brownish black back patch. That subspecies, *paludicola*, extends south only to northwestern Oregon.

INTRODUCTION

The subspecies of the Marsh Wren (*Cistothorus palustris*) in California were reviewed most recently by Rea (1986). The format of that review (Phillips 1986), however, did not allow a species with variation as complex as the Marsh Wren's to be analyzed as thoroughly as appropriate. Also, specimens collected over the last ten years now allow that variation to be described more accurately than was previously possible. Here we attempt to describe the Marsh Wren's variation as it relates to southern California and to apply the information to understanding of the species' distribution and migration. Our central goal is to place the resident Marsh Wrens of coastal southern California within the framework of the species' variation. We also attempt to describe the Marsh Wren's southern California distribution in detail, as this is still poorly understood [e.g., the map in Zeiner et al. (1990) has many inaccuracies].

In western North America, various populations of the Marsh Wren differ in color, pattern, and size. The crown ranges from entirely brown to black with only a small brown patch in the center of the forehead. The dark crown patch is separated from the black and white patch on the back by a brown collar, which ranges in width from practically zero to about 9 mm. The patch on the back ranges from small and brownish black with obscure whitish streaks to large and completely black with white streaks as broad as the black between them. The scapulars, rump, under tail coverts, and background color of the tail range from medium buffy brown to deep rufous. The underparts range from practically white to mostly buff or brown with only small pale patches on the throat and in the center of the belly. The variation in size is most easily expressed by wing length.

HISTORICAL BACKGROUND

Ridgway (1904) listed two subspecies of the Marsh Wren for California, the smaller, darker *paludicola* Baird, 1858, from the "Pacific coast district," west of the Cascade Range and Sierra Nevada (type locality Shoalwater [now Willapa] Bay, Pacific County, Washington), and the larger, paler *plesius* (Oberholser, 1897) from the "Rocky Mountain plateau district," west to northeastern California (type locality Fort Wingate, New Mexico, in the winter range). Grinnell (1903) first recognized *plesius* as a winter visitor to coastal southern California.

Swarth (1917) described *aestuarinus*, type locality Grizzly Island, Solano County, California, as darker still than *paludicola* but as large as *plesius*. He ascribed to *aestuarinus* a range extending from Suisun Bay through the San Joaquin delta and valley, with scattered specimens of migrants from more coastal localities. *Cistothorus p. paludicola* he believed resident along California's entire coastline, extending inland in the lowlands of southern California, though he cited a few inland specimens from northern California as well. Grinnell and Miller (1944) followed Swarth (1917) closely, designating coastal specimens of *aestuarinus* and inland specimens of *paludicola* as migrants. They extended the breeding range of *aestuarinus* to the Imperial and Colorado River valleys.

Aldrich (1946) subdivided *plesius*, describing a duller, less rufescent subspecies *pulverius* (type locality Sprague, Lincoln County, Washington). He ascribed to *pulverius* a breeding range from eastern Washington south to northeastern California and northwestern Nevada. The fifth edition of the American Ornithologists' Union (1957) checklist followed Grinnell and Miller (1944) for the dark lowland forms but did not distinguish *pulverius*. Phillips et al. (1964) took an even more conservative approach, reverting to Ridgway (1904) in recognizing only one dark lowland subspecies, *paludicola*, and one pale plateau subspecies, *plesius*. Monson and Phillips (1981), however, accepted *pulverius* and equivocated on *aestuarinus*.

Not until Phillips (1986) was the species as a whole revised again. In this work, Rea contributed the characterizations of the dark lowland subspecies of western Marsh Wrens, while Phillips himself covered the remainder of the species. Phillips recognized both *pulverius* and *plesius*, while Rea recognized *aestuarinus*, segregated the desert population from *aestuarinus* as *deserticola*, and suspected the coastal California population to represent an undescribed subspecies, "brighter and richer" than *paludicola*, *aestuarinus*, or *deserticola*.

Figure 1 shows the general breeding distribution of the Marsh Wren in western North America, the type localities of the named subspecies addressed in this study, and the sites in coastal southern California where Marsh Wrens were collected for this study.

METHODS

Specimen Resources

The taxonomic identity of the Marsh Wrens of coastal California cannot have been adequately assessed previously because of a dearth of specimens known to represent the local breeding populations. Migrants of *pulverius* and *plesius*, especially the latter, are common in southern California in winter, and their arrival and departure dates have not been known precisely.

The ideal specimens on which to base a taxonomic study of the Marsh Wren should be collected as soon as possible after a complete molt and therefore with the least worn plumage with its maximum genetically determined information content. The birds' constant contact with rough, often damp vegetation wears and stains the plumage more than in many species. Though in the eastern United States the Marsh Wren has a complete prealternate (prenuptial) molt in spring (Kale 1966), such a molt is not common in the West. Of 11 February–May specimens from southern California examined during this study, all are too worn to have undergone an extensive recent molt, and of the three whose molt status was described on their label, all specified "no molt." Likewise two March specimens from southwestern British Columbia [San Diego Natural History Museum (SDNHM)] are rather worn and not molting. Of eight May–June specimens from southeastern Oregon, at least four are too worn to have molted recently. But three February–March specimens from Solano County, California (Carnegie Museum of Natural History, Pittsburgh) are molting their throats, and one of these was replacing its tail (K. C. Parkes pers. comm.). Since a prealternate molt in western Marsh Wrens is rare or at least inconsistent, we based our study on specimens collected shortly after the prebasic molt, in late summer or fall.

For the resident Marsh Wrens of southern California, therefore, the ideal specimens are those collected after the completion of molt but before the arrival of migrants. For such a sample, in 1994 Unitt mist-netted Marsh Wrens at three sites along the coast of San Diego County where the species was known to breed. Birds still in juvenal plumage or heavy molt were released, while those whose molt was nearly or quite completed were collected and prepared as study skins. The field work began on 23 August and ended on 7 October, when pale migrants had clearly arrived and were outnumbering the dark local birds. In all, 24 specimens from coastal San Diego County were collected for this study.

Since 1984, for basic data on land birds' distribution and migration, Roger Higson and Unitt have been collecting in the Imperial Valley, southeastern California, whose avifauna has not been studied in detail. Over 12 years, we have accumulated 33 specimens of the Marsh Wren, on dates from 4 August to 12 February. This sample includes both representatives of the local population and migrants from farther north.

In October 1984 and September 1986, Amadeo Rea, Kem Hainebach, and Unitt visited Grizzly Island and adjacent Joice Island in the delta of the Sacramento River, collecting 30 Marsh Wrens around the type locality of *aestuarinus* (12 in October 1984, 18 in September 1986). On 12 September 1986, we also took two at Gray Lodge State Wildlife Area, Butte County.

For a sample of nominate *paludicola*, we borrowed from the Burke Museum, University of Washington (UW), 20 specimens collected in Pacific and Grays Harbor counties, Washington, on 20 September 1985, 18 November 1985, and 1 and 2 October 1986. To gain a broader sample from southern California, we borrowed 13 specimens from the San Bernardino County Museum (SBCM), 41 from the Los Angeles County Museum of Natural History (LACM), 4 from the Santa Barbara Museum of Natural History (SBMNH), 2 from the Museum of Systematics and Ecology, University of California, Santa Barbara (UCSB), and 1 from the Museum of Vertebrate Zoology, University of California, Berkeley (MVZ).

The sample of specimens on which we base our characterizations of Marsh Wren subspecies were all collected within the past 15 years. We excluded older specimens because comparison of new and old specimens revealed obvious foxing of specimens collected in the first half of the century: among the darker individuals, the rump and scapulars of all the old specimens were more rufous than the recently collected ones. Because rump and scapular color appeared to be an important variable, and we know of no means for correcting for this shift, widespread among birds, we used only the recent specimens. Once the framework was established with the recent specimens, we used a few older specimens to augment our geographical and historical perspective.

Character Assessment

The features in which the Marsh Wren varies geographically differ qualitatively, so they had to be assessed in various ways. All measurements and visual assessments were made by Unitt.

Wing chord was measured to the nearest 0.1 millimeter. Body size, as reflected in wing length, is the only feature in which the sexes differ. The mean wing chord of males, in the entire sample of specimens, was 1.06 that of females. Therefore, so that the sexes could be combined in the statistical analysis, we multiplied the measurements of the females by 1.06 to yield an adjusted result, which we used in the remainder of the analysis. In support of this adjustment, Messer ran a two-way analysis of variance on our "enlarged" sample (see below under Categorization of specimens for analysis) with wing length as the response and population of origin and sex as the explanatory variables. Residual plots showed the data to be approximately normally distributed; the ratio of the smallest

Figure 1. Approximate breeding distribution of the Marsh Wren in western North America (shading). In many areas within this range, the species occurs in only scattered localized colonies. ●, type localities of subspecies addressed in this study; ▲, sites in coastal southern California where Marsh Wrens were collected for this study.

(0.72) to the largest (2.12) standard deviation was less than 3, with most sample sizes between 10 and 15. The two smallest groups had standard deviations near 1. There was no significant interaction between the sex effect and the population-origin effect ($p > 0.05$), justifying the use of a single adjustment for sex across all groups. Had we used the estimated main effect for sex from this analysis in our adjustment, the factor would have been 1.077, a change of 1.6%. We did not feel this would affect our results materially and retained the original adjustment for simplicity. A multiplicative rather than additive factor was used to bring the females' standard deviation (2.01 in the enlarged sample) closer to the males' standard deviation (2.30 in the enlarged sample).

The width of the brown nape collar (between the black of the crown and the black of the back) was measured to the nearest

millimeter. In specimens in which the rear of the crown is brown, the crown is a darker shade than the nape collar, and in these the measurement was made from this fairly abrupt transition. The width of the collar is affected to some extent by the amount to which the neck is elongated or compressed when the specimen is prepared. A few specimens were not scored for this variable because they were poorly made or had lost neck feathers. The great majority of the California specimens were prepared by Unitt; preparation by a single technician enhances uniformity. Nape-collar width is a significant variable only in comparisons of the broad-collared *paludicola* from coastal Washington with other populations. The sample of *paludicola* consisted of specimens with naturally proportioned necks all beautifully made, largely by C. S. Wood.

The variation in crown pattern was assessed by ranking each specimen on a scale from 1 to 6, in comparison to six specimens serving as standards. In category 1 (standard SDNHM 43970) the crown is essentially entirely brown, with only a few black feathers at the sides. In category 2 (standard SDNHM 44592) the crown is mostly brown, with some black along the sides. In category 3 (standard SDNHM 44532) the black extends around the rear of the crown as well as along the sides. In category 4 (standard SDNHM 48937) the crown is about half brown and half black. In category 5 (standard SDNHM 48932) the crown is mostly black with some brown extending from the forehead into the center. In category 6 (standard SDNHM 48982) the crown is black with only a small brown patch on the forehead.

The variation in back pattern we assessed by ranking each specimen on a scale from 1 to 4. In category 1 (standard UW 40570) the back is brownish black with very narrow dull whitish streaks. In category 2 (standard SDNHM 43379) the back is deeper black with whiter but still narrow streaks. In category 3 (standard SDNHM 48992) the back is deep black with white streaks broader than in category 2 but still narrower than the intervening black streaks. In category 4 (standard SDNHM 42843) the pure white and pure black streaks are of about equal width.

The variation in the color of the scapulars and rump and of the underparts we assessed by two methods. First, Unitt ranked the color of the scapulars and rump on a scale from 1 to 10. Category 1 (standard SDNHM 43469) corresponds to a medium tawny brown, close to color 26, Clay Color, of Smithe (1975). Categories 2 (standard SDNHM 43972) and 3 (standard SDNHM 44592) are somewhat darker, the latter close to Smithe's color 121C, Mikado Brown. Category 4 (standard SDNHM 48954) is close to color 223, Verona Brown. Categories 5 (standard SDNHM 47685) and 6 (standard SDNHM 43456) are darker yet, the latter close to color 121B, Brussels Brown. Categories 7 (standard SDNHM 48937) and 8 (standard SDNHM 48938) are a deeper cinnamon-rufous, category 8 being close to Smithe's color 23, Raw Umber. Finally categories 9 (standard SDNHM 48981) and 10 (standard SDNHM 48912) are the darkest rufous, the latter close to color 121A, Prout's Brown.

Later, Théry and Unitt measured the reflectance spectrum of the rump of each specimen in percentage of a Spectralon (Ancal, Inc.) white standard, using an Ocean Optics, Inc., PS1000 diode-array portable spectroradiometer upgraded for near-ultraviolet light (range 300–800 nm), a bifurcated fiber-optic reflectance probe, and an Ocean Optics LS-1 tungsten–halogen lamp. To avoid specular reflectance, measurements with the reflectance probe were done at an angle of 45° against the feather surface, measuring an oval spot 3 mm wide. One measurement was made at the center of the rump for each specimen, as long as the reflectance curve averaging 5 scans was stable. Reflectance spectra were recorded between 350 and 700 nm with a resolution of 1 nm. The measurement range includes some near-ultraviolet light that is not perceived by humans but is by many birds. From reflectance curves, Théry then assigned each recorded spectrum a score for hue (dominant wavelength), chroma (purity or saturation of the color), and total brightness, computed following Endler (1990).

Our procedure with underpart color was parallel to that for rump and scapular color. The specimens were ranked among six categories. In category 1 (standard SDNHM 43972) the breast is practically white with a light buff tinge only along the sides. In category 2 (standard SDNHM 44592) a faint buff wash extends across the breast. Specimens in category 3 (standard SDNHM 47685) have a distinct buff breast band. In category 4 (standard SDNHM 48912) the breast is darker brownish buff and the throat is tinged brown. In category 5 (standard SDNHM 48938) the breast is still darker, medium brownish. Category 6 (standard SDNHM 43386) represents the Marsh Wrens with the darkest breasts; the entire underparts are brown with only a triangular patch in the center of the belly being whitish. In the darker-breasted specimens collected very shortly after molt, in September, the underparts are more rufous, whereas in those from the same locality collected just one month later, in October, the color has dulled to a drab medium brown. Because this change appears to result from some adventitious process, the specimens were ranked for underpart color on the basis of paleness or darkness alone, not hue.

Again, we evaluated the breast color of each specimen with a spectroradiometer, placing the sensor over the darkest point along the midline of the breast. The results were converted into values for hue, brightness, and chroma in the same way as those for the rump.

Data Analysis

Spectroradiometry. A graphical assessment of the spectroradiometric results for breast and rump color suggested that brightness was the variable with the greatest (and probably only) systematic variation. Scatterplots of spectroradiometric assessment versus visual ranking for rump/scapular brightness and for breast brightness (Figures 2 and 3) reveal in both cases a positive but only moderate correlation (Pearson correlations of 0.51 and 0.58, respectively). Some difference might be expected because the spectroradiometer measured a range of wavelengths broader than that to which the eye is sensitive, but there may be other confounding factors as well. Because the visual assessments consistently gave better results, we did not use the spectroradiometric results further in the analysis.

The reason(s) why the spectroradiometer proved less satisfactory than the eye in these comparisons are unclear. Endler (1990) discussed several reasons why the human eye's and brain's perception of colors is not proportional to the electromagnetic characteristics of the light reflected from an object and reaching the eye. He recommended the use of spectroradiometers to circumvent this problem. He did not address, however, other problems that may affect the applicability of spectroradiometers in taxonomic studies of birds, where often subtle rather than gross contrasts require quantification and testing. We suspect that such problems more than the nonlinear response of the human eye and brain accounted for the mediocre agreement between the spectroradiometric and visual assessments in our study. Possibly variation arising from the irregularly multilayered structure of plumage overwhelmed the rather subtle variation in color we were trying to record. Though we tried to ensure that the sensor recorded only the pigmented tips of the feathers, possibly it was influenced irregularly by some of the dark gray bases of the feathers, confusing the results. The sensor read a much smaller area of plumage than that embraced by the visual assessments; possibly because of differences of scale the two are not always comparable. The low reflectance of the rump and the dullness of both the rump and breast colors may exceed the equipment's sensitivity. Though spectroradiometry of plumage has been used occasionally in taxonomic studies of birds (e.g., Johnson 1980, Atwood 1988), to our knowledge, the reliability and sensitivity of various spectroradiometers and various techniques for using them have not been compared and tested. Since more precise and replicable quantifications

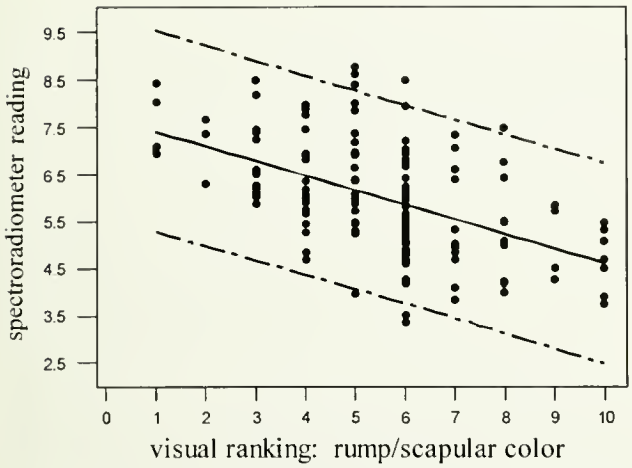

Figure 2. Scatterplot of visual rankings of Marsh Wren rump/scapular color versus brightness of rump as specified by the spectroradiometer. The solid line is the regression line; the dotted lines enclose the 95% prediction interval, predicting the spectroradiometer reading from the visual ranking. The plot shows a positive but moderate correlation (Pearson correlation of 0.51).

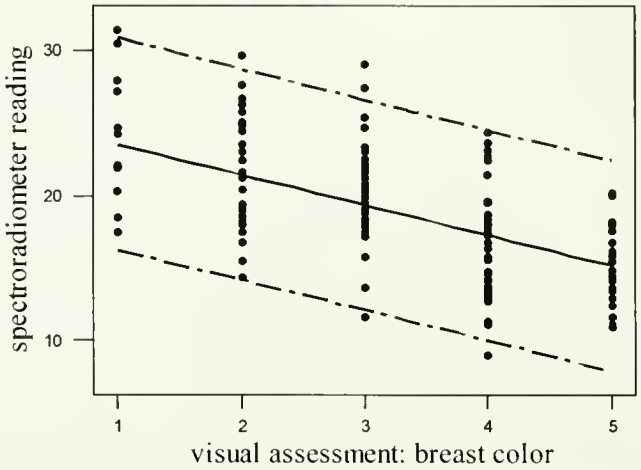

Figure 3. Scatterplot of visual ranking of Marsh Wren breast color versus brightness of breast as specified by the spectroradiometer. The solid line is the regression line; the dotted lines enclose the 95% prediction interval, predicting the spectroradiometer reading from the visual ranking. The plot shows a positive but moderate correlation (Pearson correlation of 0.58).

of plumage color are obviously desirable, such testing is warranted. N. K. Johnson (pers. comm.) found that a Bausch & Lomb 505 and a Minolta CR 300 both detected the most subtle differences visible to the eye. Zuk and Decruyenaere (1994) reported that a Li-Cor LI-1800 spectroradiometer, used on rooster combs and single feathers glued to a card, gave better results than visual matching to Munsell color samples. The visual assessments, however, were "constrained by the available color standards." Because of the difference in texture, matching plumage colors to flat color samples is difficult. Use of specimens themselves as standards circumvents this. One reason that Endler (1990) urged that color be measured electronically is that insofar as possible color differences should be evaluated from the animal's point of view. In studies of sexual selection or social behavior this is clearly important. But human taxonomists are responsible for classifications, so in this field human perception remains relevant. Electronic techniques may ultimately yield better means of expressing the colors of birds, but we felt the questions about them were still too great for the more traditional visual method to be abandoned in this case.

Categorization of specimens for analysis. Messer and Unitt entered the measurements of wing chord and nape-collar width and the rankings of crown pattern, back pattern, underpart pattern, and rump/scapular color into a computer database. We apportioned the specimens among three categories: a core sample of specimens certain to represent particular breeding populations, an enlarged sample including additional specimens inferred to represent those populations, and the remaining specimens, whose allocation was ambiguous.

The core sample consisted of 72 specimens we are certain to represent one of five key populations. For 65 of these, all six variables could be assessed; seven were defective in one or more characters so had to be excluded from some analyses. First, the core sample included 10 specimens of *plesius/pulverius*, from the Great Basin or from sites in Arizona where there are no breeding Marsh Wrens, under the assumption that only *plesius/pulverius* are long-distance migrants likely to reach central Arizona. Second, the core sample included all 20 specimens from the Willapa Bay area of Washington, taken to represent the breeding population around the type locality of *paludicola*, under the assumption that migration of *plesius/pulverius* from east of the Cascades is largely or entirely southward rather than due west. Jewett et al. (1953) did not report any migration of the inland subspecies to western Washington, supporting this assumption. Third, the core category included 19 early September specimens from the type locality of *aestuarinus* (five of these were defective in one or more characters). Fourth, it included five late August and September specimens from the Imperial and lower Colorado River valleys, including the two cotypes of *deserticola*. Two of these five were molting the outer primaries so could not be used in comparisons including wing length. Finally, it included 18 specimens from coastal San Diego County. Seventeen of these were collected in late August and September, and included all specimens in this interval save one taken on 23 September, which from its conspicuously paler color and larger size we inferred to be a migrant *plesius/pulverius*. The 18th specimen, collected on 28 February 1984, had enlarged testes (left 5.5 × 4.5 mm), beyond the size expected in a winter visitor.

This core sample was assessed by both cluster and discriminant function analysis (see below).

The enlarged sample consisted of the original core sample of birds whose population of origin was certain plus additional specimens whose origin could be confidently inferred. Nevertheless, we have distinguished these additional specimens from the core-sample specimens in all our comparisons. Twenty-nine additional specimens from the Colorado Desert we assumed to be either local residents or migrants from the Great Basin, the other western populations being sedentary. We allocated these desert specimens by means of a linear discriminant-function analysis confined to the core *plesius/pulverius* sample plus all specimens from the Colorado Desert. We used the discriminant function based on the core specimens to classify the remaining specimens into the two categories. A canonical variable plot (Figure 4) shows a clean separation though no gap between the two categories and a wide separation between the core samples. Therefore, we defined an enlarged desert sample of 18 specimens. The remaining 16 Imperial Valley specimens we grouped with the core sample of *plesius/pulverius* to constitute an enlarged plateau sample of 26 specimens. If any specimens of *deserticola* were misplaced with *plesius/pulverius* they could only degrade any separability of the plateau subspecies from any of the darker lowland subspecies.

We repeated this procedure with the October sample from the Sacramento delta, again under the assumption that the only migrant Marsh Wrens likely to reach this area are *plesius/pulverius*. All 12 of the October specimens clustered tightly with the 14 core September

Figure 4. Histogram of the canonical variable resulting from a stepwise discriminant analysis of the core sample of 10 specimens of *Cistothorus palustris plesius/pulverius* and all Marsh Wren specimens from the Imperial and lower Colorado River valleys. The discriminant function was based on the core specimens, and was used to classify the remaining specimens. Rump/scapular color, underpart color, wing length, and crown pattern, in decreasing order of importance, are the informative variables. C, core specimens of *plesius/pulverius*; D, core specimens of *deserticola*; A, inferred specimens of *plesius/pulverius*; B, inferred specimens of *deserticola*.

specimens, and this cluster was well separated from the *plesius/pulverius* sample (Figure 5), so we enlarged the core September delta sample by adding the October sample.

These two steps generated the enlarged sample of 113 specimens, constituting the second level of inclusiveness. Nine of these could not be scored for one or more characters and had to be omitted in comparisons such as the discriminant-function analysis of all populations simultaneously.

Finally, we applied the discriminant functions derived from both the core and enlarged samples to the 26 remaining specimens. These specimens are from sites away from those of our five "parent" populations (coastline from southern Oregon to Ventura County; oases of Mojave Desert). This procedure allowed us to suggest a taxonomic placement for those specimens.

Statistical Procedures

Cluster analysis. With the core sample (excluding defective individuals) of 65 specimens, Messer ran cluster analyses in MINITAB, version 10 xtra, using a hierarchical agglomerative algorithm. Distances were computed by means of Ward's method, which finds clusters with minimum within-cluster sums of squares (Afifi and Clark 1984: 393). We present results using unstandardized variables; results for standardized variables were similar.

Discriminant Analysis. Messer ran discriminant analyses in BMDP386, version 1990, program 7M. The default stepwise procedure was used in all cases. Scatterplots of the original variables and canonical variable plots were produced in MINITAB, the latter using the output from BMDP.

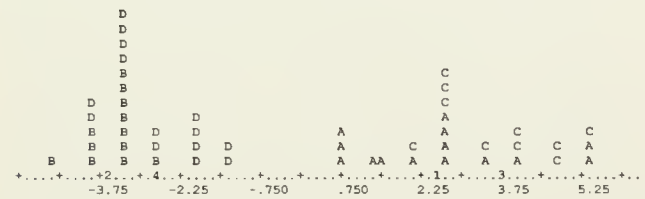

Figure 5. Histogram of the canonical variable resulting from a stepwise discriminant analysis of the core sample of 10 specimens of *Cistothorus palustris plesius/pulverius* and all Marsh Wren specimens from the San Joaquin delta. The discriminant function was based on the core specimens, and was used to classify the remaining specimens. Underpart color, rump/scapular color, wing length, back pattern, and crown pattern, in decreasing order of importance, are the informative variables. C, core specimens of *plesius/pulverius*; D, core specimens of *aestuarinus*; A, inferred specimens of *plesius/pulverius*; B, inferred specimens of *aestuarinus*.

We applied stepwise discriminant analysis to the initial core sample, once with the three nondefective Colorado Desert specimens and once without them, to assess the degree of differentiation among the five key populations. We followed this by a parallel procedure with the enlarged sample. In addition, we compared each of the five populations with each of the others, a total of ten pairwise comparisons. These comparisons allowed us to evaluate and rank the characters distinguishing each of the populations.

Results are presented in terms of correct classification rates, estimated by means of the jackknife procedure in BMDP. This procedure adjusts the estimated rate downward in an attempt to correct for overly optimistic estimates that arise because the same specimens are used in both the construction of the classification rule (the discriminant function) and the assessment of how well if performs (the classification rates). In addition, in the pairwise comparisons the discriminant function was computed on the basis of the core sample only and was then applied to both the core sample and the additional inferred specimens when present. In all comparisons except the two between *plesius/pulverius* and either *deserticola* or *aestuarinus* (which were used in classifying some of those inferred specimens) the additional specimens may be considered an independent test sample, although not a randomly selected one. Thus the classification rates of the inferred specimens constitute additional evidence for or against group separation.

We felt that the distance between groups was best presented graphically in terms of scatterplots of all the data. In all cases, the F statistic for a test of equality of group means was significant at $p < 0.005$, but because of the stepwise procedure used in variable selection, the nonnormal nature of several of the variables, and the nonrandom nature of the samples, it is questionable how much inference may be drawn from this fact. For similar reasons, we decline to present confidence regions or prediction regions based on an assumption of normality.

For ease of interpretability in the pairwise comparisons, we present graphs in terms of the pair of variables that we felt were most useful in making a visual assessment of the group separation. This is usually the pair of variables with the strongest univariate group mean separations (as measured by the F-to-enter test statistics at step 0 in the stepwise variable-selection procedure). Occasionally, this pair did not produce the most obvious separation, and in that case the pair of variables that, considered together, was most informative was used (as measured by the F-to-enter test statistic at step 1 in the variable-selection procedure). In the figure legends, these are described as "the pair of variables in which [the groups] differ most." While these plots are more easily interpretable than the corresponding canonical-variable plots, they do not separate the groups as well (compare Figures 4 and 11).

In assessing which characters were most informative in the pairwise comparisons, we again chose to present them in order of univariate mean group separations, as we felt these would be the easiest to use visually. Note that this means the first two variables listed may not be the *pair* of most informative variables but rather the two variables that when considered in isolation best differentiate the groups. When we say a pair of populations "differs significantly" in a variable, we mean the group means differ significantly at $p < 0.05$. The variables actually used in the discriminant function are indicated by italics. These are the variables that, when the others are already in use, contribute *additional* information.

RESULTS

Cluster Analysis

Cluster analysis of the initial core sample of 65 specimens, covering all five key populations, identified three well-defined groups (Figure 6). The sample from coastal San Diego County was the most distinct; the 10 specimens of *plesius/pulverius* formed a second branch. Among the remainder of the specimens, the coastal Washing-

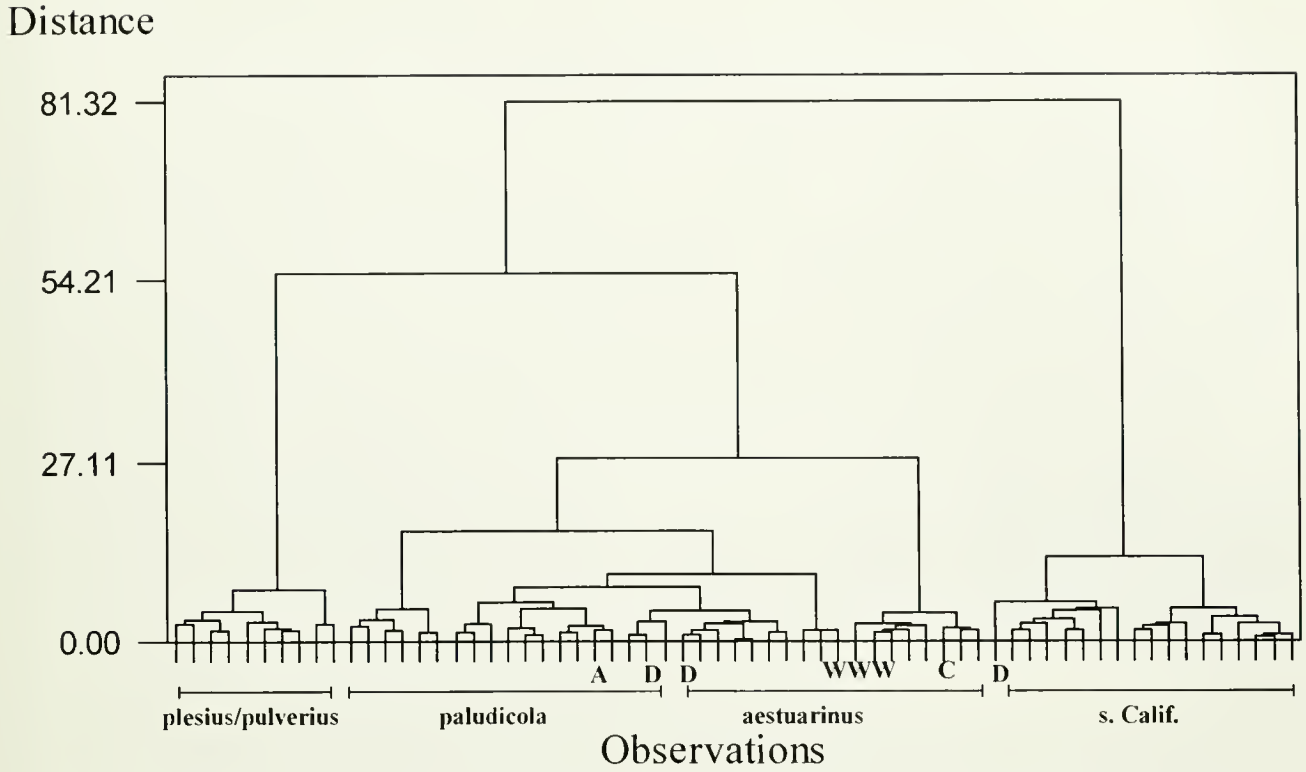

Figure 6. Cluster analysis of the core sample of 65 specimens of the Marsh Wren, covering all five key populations on which further analyses were based. Letters designate exceptional specimens not clustering with the rest of their population as labeled. A, *aestuarinus*; C, coastal southern California; D, *deserticola*; W, *paludicola*. The height of the horizontal bar separating each cluster is proportional to the distance between clusters, as measured by Ward's algorithm. The first dichotomy separates all but one of the coastal southern California sample from the remaining specimens; the second dichotomy separates the Great Basin population (*plesius/pulverius*) from the remaining specimens. The population of southwestern Washington (*paludicola*) segregates only partially from the remaining specimens, from the Colorado Desert (*deserticola*) and San Joaquin delta (*aestuarinus*).

ton (*paludicola*) and Sacramento Delta (*aestuarinus*) samples clustered together but did not segregate clearly from each other, some *paludicola* forming a subcluster, others falling with *aestuarinus*. Of the three Colorado Desert (*deserticola*) two fell among the cluster of *aestuarinus*, one with the sample from San Diego.

The sharp distinction of the San Diego sample from the remaining specimens suggested that it be evaluated as a separate group in the discriminant analyses; we then used the results of these analyses, both of the entire sample and of comparisons to each other population individually, to assess the level of and basis for this distinction.

Discriminant Analysis: All Five Populations Simultaneously

Core sample, deserticola *excluded.* The core sample consisted of specimens that we are certain, on the combined basis of their locations and dates, to represent one of our five key or "parent" populations, corresponding to either named subspecies or the resident population of coastal southern California. Because the core sample included only three complete specimens of *deserticola*, possibly insufficient to define a discrete group, we ran the analysis both with and without these three specimens. Discriminant analysis of the core sample containing only the remaining four groups yielded a function capable of categorizing 58 of the 62 specimens into the four groups defined by their origins, for an overall correct classification rate of 94%. The San Diego and Great Basin samples did not overlap with any other; the only misclassification was between *paludicola* and *aestuarinus*. When the classification rates were corrected via the jackknife procedure, the results differed only in that one specimen from the San Diego sample and an additional specimen of *paludicola* were misclassified with *aestuarinus* (Table 1). From 86 to 100% of each group was classified as its origin suggested; for each of the four groups this figure exceeds the 75% traditionally regarded as the threshold for formal taxonomic recognition, suggesting each of the four may constitute a valid subspecies. A plot of the two most informative canonical variables associated with the discriminant function (Figure 7) best illustrates the segregation among the populations, reducing to two dimensions most of the information from the six variables with which we describe variation in western Marsh Wrens.

Core sample, deserticola *included.* A repetition of the discriminant analysis including the three August/September specimens from

TABLE 1. Jackknife-corrected discriminant-function classification of the core samples representing *Cistothorus palustris plesius/pulverius*, *C. p. paludicola*, *C. p. aestuarinus*, and the population of coastal southern California.

	Number of specimens classified as				
	plesius/ pulverius	*palu- dicola*	*aestu- arinus*	Coastal S. Calif.	Percent Correct
C. p. plesius/ pulverius	10	0	0	0	100.0
C. p. paludicola	0	18	2	0	90.0
C. p. aestuarinus	0	2	12	0	85.7
Coastal S. Calif.	0	0	1	17	94.4

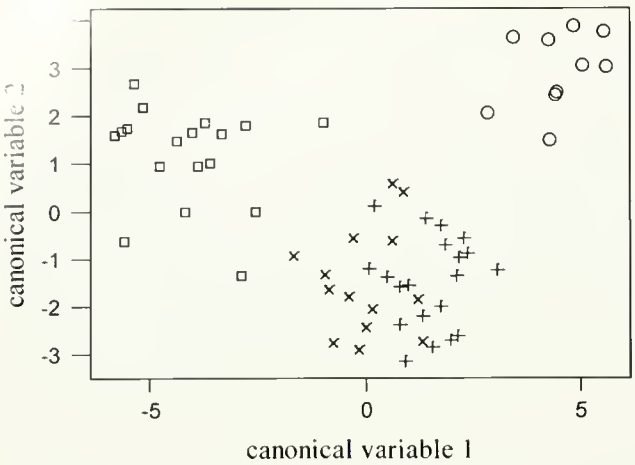

Figure 7. Scatterplot of the two most informative canonical variables generated by a stepwise discriminant analysis of the core sample of 62 specimens of the Marsh Wren, covering four key populations (*deserticola* excluded). ○, specimens from the Great Basin or inferred to have originated there (*plesius/pulverius*); +, specimens from southwestern Washington (*paludicola*); ×, specimens from the San Joaquin delta (*aestuarinus*); □, specimens from coastal southern California.

the Colorado Desert did not greatly alter the results among the other four populations, but the attempt to define a group on the basis of these three specimens alone was unsuccessful. With the jackknife procedure, two of the three were classified by the discriminant function among other groups, while the desert "cluster" attracted one or two specimens from each of the other groups except *plesius/pulverius*. A plot of the canonical variables implies a tendency of the Colorado Desert population, despite its marginal position geographically, to be intermediate among the other four clusters in plumage. Clearly, a larger sample from the Colorado Desert was necessary for the taxonomic position of that population to be assessed, and this was the goal of the following step.

Enlarged sample. We repeated the discriminant analysis, with an attempt to define five populations, on the core sample augmented as described above under Categorization of specimens for analysis (including the 12 October specimens from the San Joaquin delta, all inferred to represent *aestuarinus*, the additional 13 and 16 specimens inferred, respectively, from comparison of *deserticola* and *plesius/pulverius* to represent those populations; Figure 4). This analysis of 104 specimens (Figure 8) suggested that all five populations could be considered subspecies. The poorest distinction was between *aestuarinus* and *deserticola*, but even after jackknife correction the discriminant function still classified 81% of each of these groups as expected (Table 2).

Discriminant Analysis: Pairwise Comparisons of Five Populations

Cistothorus p. plesius/pulverius vs. *paludicola*. This pair of populations differs significantly in all variables, in order of decreasing importance, *wing length*, *rump/scapular color*, underpart color, back pattern, *nape-collar width*, and crown pattern. The discriminant function revealed a wide separation between *paludicola* and the core sample of *plesius/pulverius*. With the enlarged sample of *plesius/pulverius*, the separation was not complete; three specimens fell within the cluster of *paludicola*, reducing the rate of correct classification in the total sample to 93% after correction for overclassification via a jackknife procedure. Figure 9, a scatterplot of *plesius/pulverius* versus *paludicola* in wing length versus rump/scapular color, reveals these three misclassified specimens. Possibly, some of the misclassified *plesius/pulverius* in the enlarged sample, from the Imperial Valley, were misidentified *deserticola* (see above under Categorization of specimens). But even if not, the two populations are differentiated well enough to be continued to be recognized as subspecies.

Cistothorus p. plesius/pulverius vs. *aestuarinus*. This comparison yielded one of the strongest distinctions; the two groups differ significantly in five of six variables (all except nape-collar width), and the discriminant analysis, after jackknife correction, classified 100% of the specimens as expected. Rump/scapular and underpart color are the two variables most responsible for this separation (Figure 10).

Cistothorus p. plesius/pulverius vs. *deserticola*. These two groups differ significantly in four variables (*rump/scapular color*, *underpart color*, wing length, and crown pattern), but in the discriminant analysis the second two did not add any discriminating power beyond the first two. Therefore, in Figure 11 we present a scatterplot of the two groups in just these two variables; this allowed us to include the two specimens in the core sample of *deserticola* that were molting their primaries. In this plot, the groups appear well separated, but, as discussed above under Categorization of specimens and shown in Figure 4, several fall and winter specimens from the Imperial Valley bridge the gap. Study of a larger sample of both subspecies may reveal some overlap not evident with our core samples. Nevertheless, the strong separation obvious in Figure 11, and the 100% separation achieved by the discriminant function, even after jackknife correction, implies that any overlap is not extensive enough to invalidate the distinction between *deserticola* and *plesius/pulverius*.

Cistothorus p. plesius/pulverius vs. coastal southern California

TABLE 2. Jackknife-corrected discriminant-function classification of the enlarged samples representing *Cistothorus palustris plesius/pulverius*, *C. p. paludicola*, *C. p. aestuarinus*, *C. p. deserticola*, and the population of coastal southern California.

	Number of specimens classified as					
	plesius/pulverius	*paludicola*	*aestuarinus*	*deserticola*	Coastal S. Calif.	Percent Correct
C. p. plesius/pulverius	22	1	0	1	0	91.7
C. p. paludicola	0	17	2	1	0	85.0
C. p. aestuarinus	0	2	21	3	0	80.8
C. p. deserticola	0	0	2	13	1	81.3
Coastal S. Calif.	0	0	0	1	17	94.4

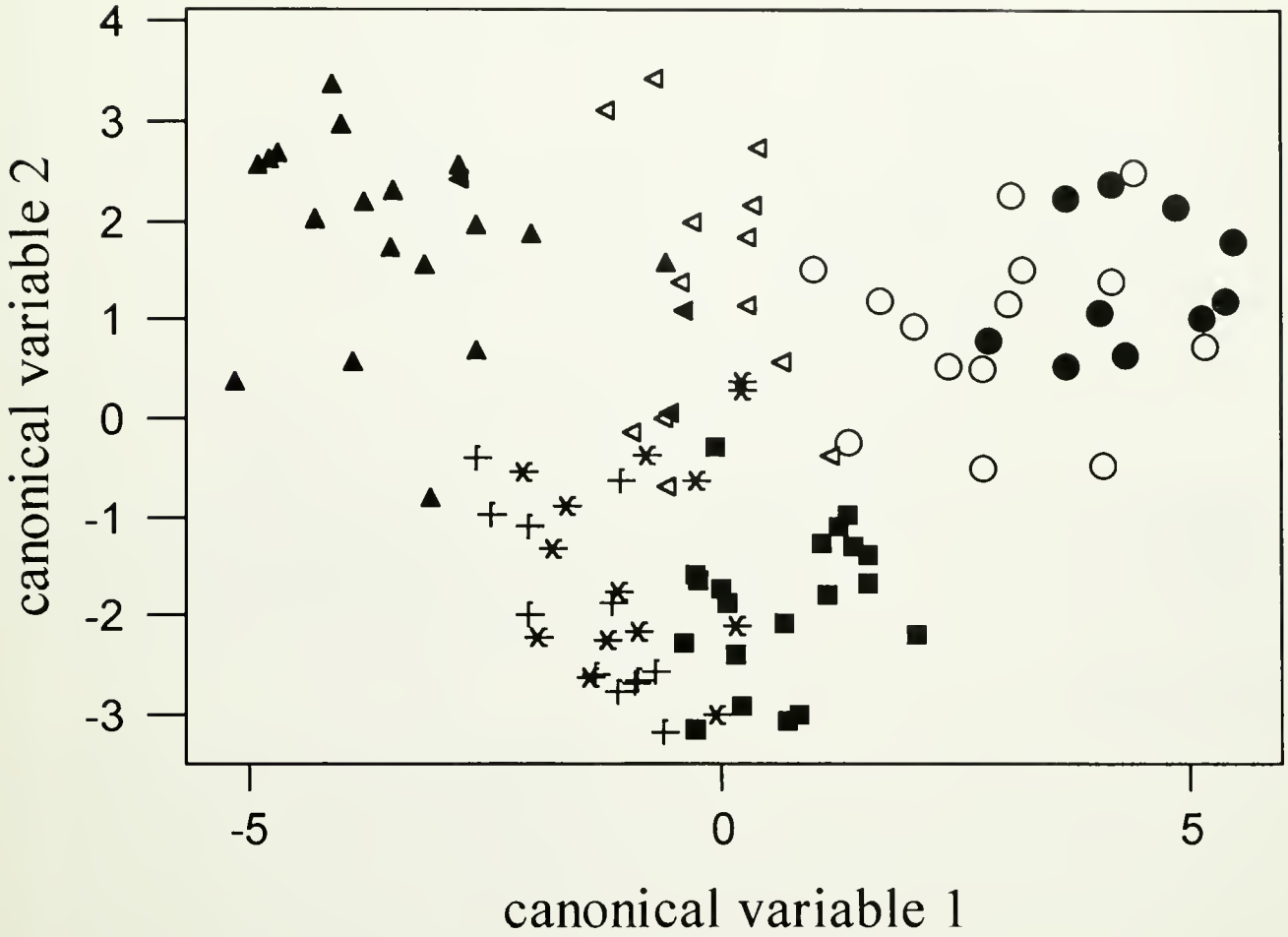

Figure 8. Scatterplot of the two most informative canonical variables generated by a stepwise discriminant analysis of the enlarged sample of 104 specimens of the Marsh Wren, consisting of the core sample of 65 specimens augmented with 14 inferred specimens of *plesius/pulverius*, 12 inferred specimens of *aestuarinus*, and 13 inferred specimens of *deserticola*. ●, core-sample specimens of *plesius/pulverius*; ○, inferred specimens of *plesius/pulverius*; ■, specimens from southwestern Washington (*paludicola*); *, core-sample (September) specimens from the San Joaquin delta (*aestuarinus*); +, inferred (October) specimens of *aestuarinus* from the San Joaquin delta; ◀, core-sample specimens from the Colorado Desert (*deserticola*); ◁, inferred specimens of *deserticola* from the Colorado Desert; ▲, core-sample specimens from coastal southern California.

population. *Rump/scapular color*, *wing length*, underpart color, and *crown pattern* all contributed significantly toward the strong separation of these two groups. Figure 12 is a scatterplot based on the two strongest variables, rump/scapular color and wing length. Only two specimens were misclassified by the discriminant function. Both are inferred specimens of *plesius/pulverius* from the Imperial Valley and not used in the generation of the discriminant function.

Cistothorus p. paludicola vs. *aestuarinus*. Five variables contributed significantly toward the differentiation of the Washington and San Joaquin Delta samples: in order of decreasing importance, *underpart color*, *nape-collar width*, crown pattern, rump/scapular color, and back pattern. Figure 13, a scatterplot depicting the first two of these variables, reveals some overlap. Even with all variables combined in a discriminant function, however, a 100% separation could not be achieved. Marginal overlap left three specimens of *paludicola* and one of *aestuarinus* on either side of the line of best separation decided by the discriminant function. Jackknife correction of the function suggested that 88% of the combined samples could be assigned correctly. All of the inferred (October) specimens of *aestuarinus* were correctly classified. Though the separation is not total, it appears adequate to support continued recognition of *aestuarinus* as distinct from *paludicola*.

Cistothorus p. paludicola vs. *deserticola*. *Rump/scapular color*, nape-collar width, and *back pattern* contributed toward a good separation between this pair of samples (Figure 14). Only one specimen was misclassified by the discriminant function, an inferred specimen of *deserticola* that by virtue of its rather narrow white back streaks (rated 2) and rather pale rump (rated 5), and despite its narrow nape collar (3 mm, outside the range of *paludicola*), fell in the middle of the cluster of *paludicola* as defined by the canonical variable generated by the discriminant function. Following the jackknife correction, the discriminant function predicted a 97% separation of these two populations.

Cistothorus p. paludicola vs. coastal southern California population. This pair of samples segregated 100%, differing significantly in all variables, in order of decreasing difference, *rump/scapular color*, crown pattern, wing length, *nape-collar width*, *back pattern*, and underpart color. The plot of rump/scapular color versus back pattern (Figure 15) shows the clearest separation in two variables. The canonical variable generated by the discriminant function suggested

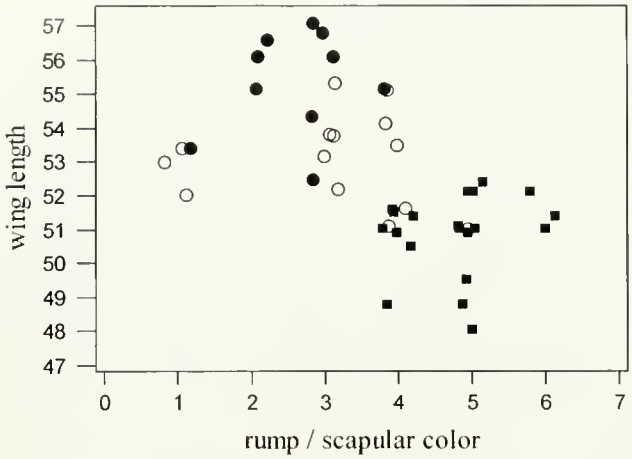

Figure 9. Scatterplot for *Cistothorus palustris plesius/pulverius* and *C. p. paludicola* of the two variables in which they differ most, wing length and rump/scapular color. So that the sexes could be considered together in one statistical process, the wing chords of females were multiplied by 1.06, the factor by which the average male Marsh Wren exceeds the average female. ●, core-sample specimens of *plesius/pulverius*; ○, inferred specimens of *plesius/pulverius*; ■, specimens from southwestern Washington (*paludicola*). In this and subsequent figures in which one or both of the axes represents a variable ranked in discrete categories, some "jitter" has been added to avoid overstrikes and thereby show all points plotted.

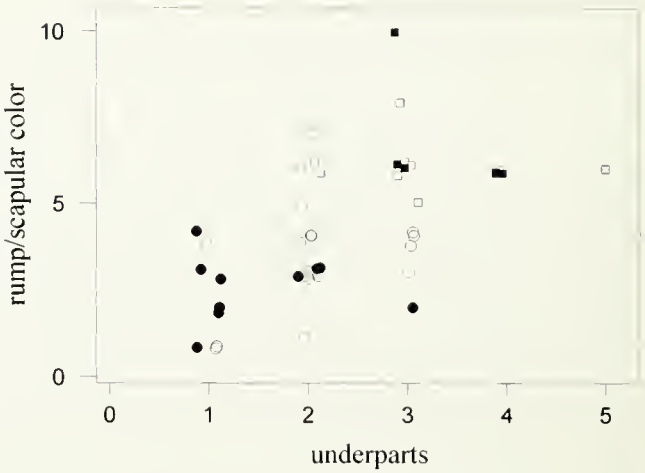

Figure 11. Scatterplot for *Cistothorus palustris plesius/pulverius* and *C. p. deserticola* of the two variables in which they differ most, rump/scapular color and underpart color. ●, core-sample specimens of *plesius/pulverius*; ○, inferred specimens of *plesius/pulverius*; ■, core (August/September) specimens of the breeding population of the Colorado Desert (*deserticola*); □, additional October–February specimens from the Colorado Desert inferred as *deserticola* (see Figure 4).

not only complete separation but a gap between the two populations (Figure 16). It is evident that the name *paludicola* does not apply to the resident Marsh Wrens of coastal southern California.

Cistothorus p. aestuarinus vs. *deserticola*. Among the 10 pairs of "parent" populations, this comparison yielded the weakest separation. The stepwise variable-selection procedure used only a single variable, *underpart color*, in the discriminant function. Back pattern is the next most informative variable; its distribution among so few categories reduces its contribution to the generation of the discriminant function. When the function was modified to include back pattern, however, it placed 3 of the 30 specimens of *aestuarinus* with *deserticola*, 1 (not from the core sample of 5 specimens) of the 18 specimens of *deserticola* with *aestuarinus* (Figure 17). Thus a distinction can be drawn so that only 4 of 48 specimens in the samples from at or near the type localities overlap, suggesting a valid distinction between these two subspecies. Application of the discriminant functions to specimens from elsewhere in California, however, mud-

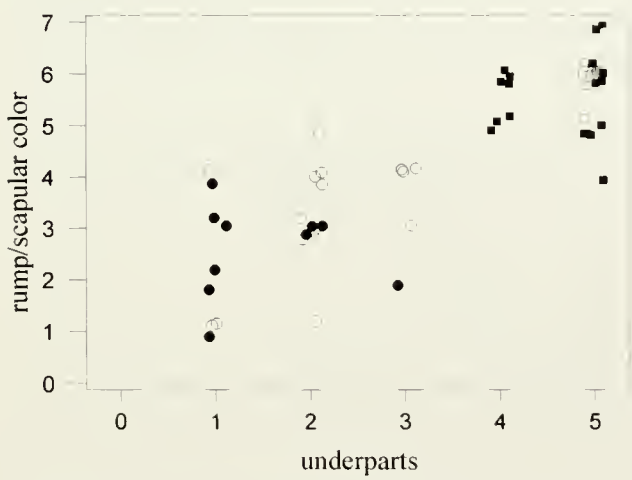

Figure 10. Scatterplot for *Cistothorus palustris plesius/pulverius* and *C. p. aestuarinus* of the two variables in which they differ most, underpart color and rump/scapular color. ●, core-sample specimens of *plesius/pulverius*; ○, inferred specimens of *plesius/pulverius*; ■, core-sample (September) specimens from the San Joaquin Delta (*aestuarinus*); □, additional (October) specimens from the San Joaquin Delta (inferred *aestuarinus*).

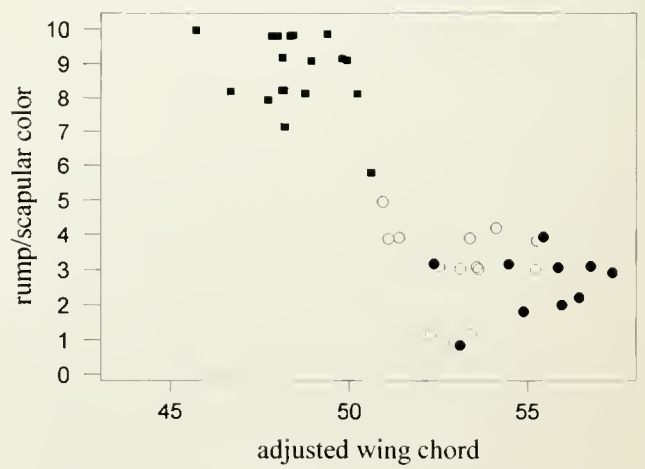

Figure 12. Scatterplot for *Cistothorus palustris plesius/pulverius* and coastal southern California Marsh Wrens of the two variables in which they differ most, rump/scapular color and wing length. So that the sexes could be considered together in one statistical process, the wing chords of females were multiplied by 1.06, the factor by which the average male Marsh Wren exceeds the average female. ●, core-sample specimens of *plesius/pulverius*; ○, inferred specimens of *plesius/pulverius*; ■, specimens of the breeding population of coastal southern California.

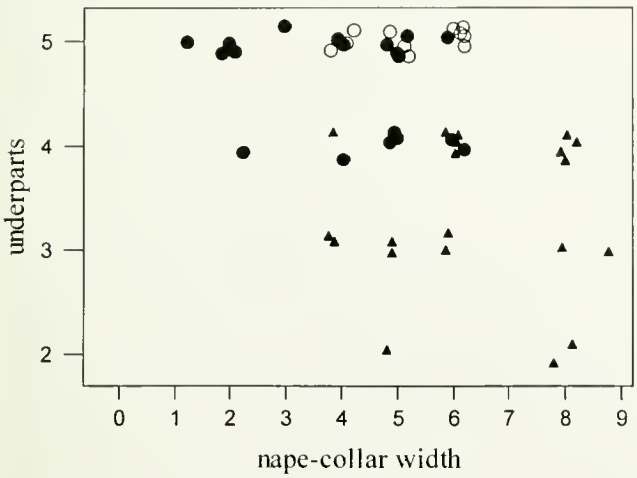

Figure 13. Scatterplot for *Cistothorus palustris paludicola* and *C. p. aestuarinus* of the two variables in which they differ most, underpart color and nape-collar width. ▲, specimens from southwestern Washington (*paludicola*); ●, core-sample (September) specimens from the San Joaquin Delta (*aestuarinus*); ○, additional (October) specimens from the San Joaquin Delta (inferred *aestuarinus*).

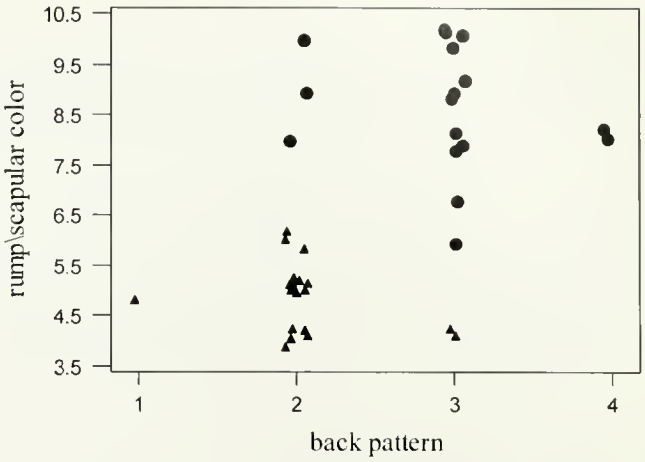

Figure 15. Scatterplot for *Cistothorus palustris paludicola* and coastal southern California Marsh Wrens of the pair of variables in which they differ most, rump/scapular color and back pattern. ▲, specimens from southwestern Washington (*paludicola*); ●, specimens of the breeding population of coastal southern California.

died this distinction substantially, so it does not seem useful on a broader scale (see below).

Cistothorus p. aestuarinus vs. coastal southern California population. The discriminant function analysis, with jackknife correction, separated these two groups completely, with a substantial gap between them. *Rump/scapular color, wing length, underpart color, crown pattern*, and back pattern, in decreasing order, all differed significantly. Figure 18, a plot of rump/scapular color versus underpart color, shows this separation in just two variables. Evidently, the name *aestuarinus* does not apply to the Marsh Wrens of coastal southern California.

Cistothorus p. deserticola vs. coastal southern California population. The discriminant analysis, from the direct result and after cross-validation via jackknifing, classified 38 and 37, respectively, of 39 specimens as expected on the basis of their origins. The discriminant-function analysis identified four variables as informative in making this distinction, in order of decreasing importance, *wing length, rump/scapular color, crown pattern*, and *underpart color*. Between this pair of populations, back pattern and nape-collar width do not differ significantly. Wing length alone separates the samples totally (with adjustment for sex, the coastal sample measures 44.0–50.4 mm, the desert sample 50.7–55.9 mm), though the approach is so close some overlap should be expected in large samples. Though the two groups differ substantially in rump/scapular color (only 2 of 18 desert specimens rating darker than 7; only 2 of 18 coastal specimens rating paler than 8, and one of these, collected in February, was likely faded in comparison to the rest of the sample, collected in August and September), the computer-

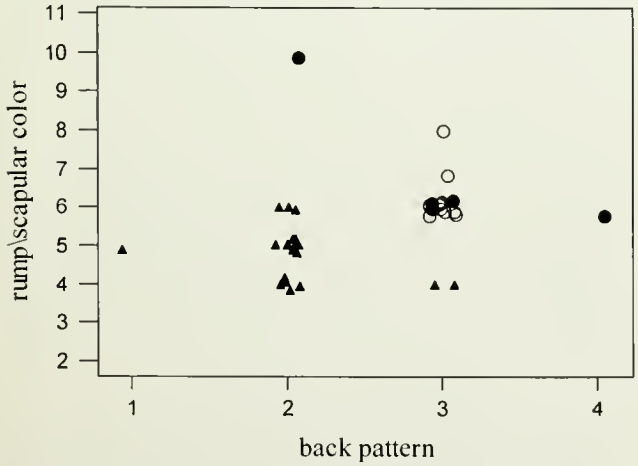

Figure 14. Scatterplot for *Cistothorus palustris paludicola* and *C. p. deserticola* of the pair of variables in which they differ most, rump/scapular color and back pattern. ▲, specimens from southwestern Washington (*paludicola*); ●, core-sample (August/September) specimens of the breeding population of the Colorado Desert (*deserticola*); ○, additional October–February specimens from the Colorado Desert inferred as *deserticola* (see Figure 4).

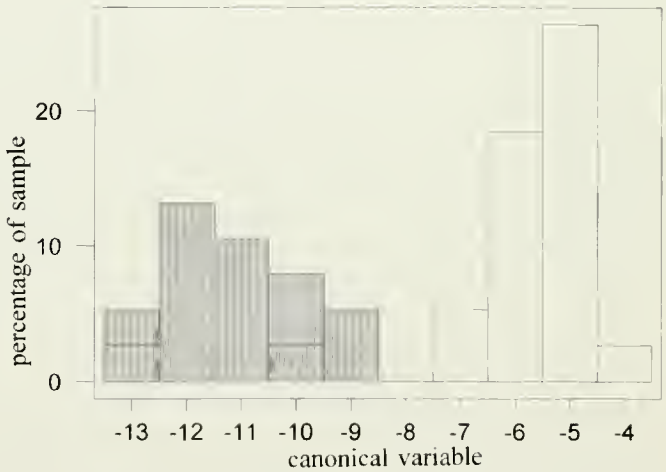

Figure 16. Histogram of the canonical variable resulting from a stepwise discriminant analysis of *Cistothorus palustris paludicola* and coastal southern California Marsh Wrens. Rump/scapular color, nape-collar width, and back pattern are the variables contributing to the separation. Shaded bars, *C. p. paludicola*; white bars, coastal southern California Marsh Wrens.

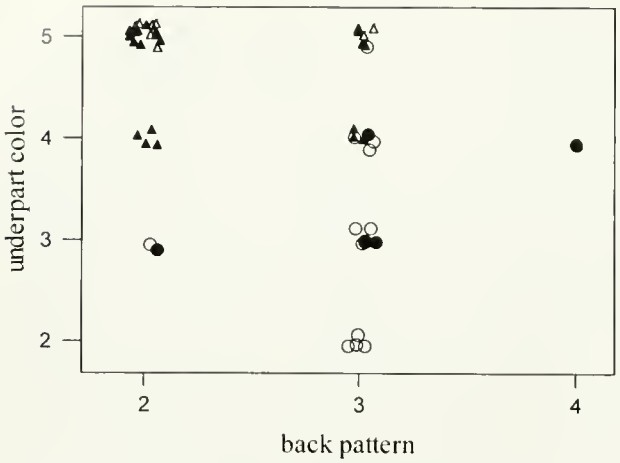

Figure 17. Scatterplot for *Cistothorus palustris aestuarinus* and *C. p. deserticola* of the only two variables in which they differ significantly, underpart color and back pattern. ▲, core (September) specimens from the San Joaquin Delta (*aestuarinus*); △, additional (October) specimens from the San Joaquin Delta (inferred *aestuarinus*); ●, core (August/September) specimens of the breeding population of the Colorado Desert (*deserticola*); ○, additional October–February specimens from the Colorado Desert inferred as *deserticola* (see Figure 4).

generated discriminant function did not use this variable, the information it provides being redundant with that for other variables. The difference in the crown is the coastal sample's averaging more extensively black. A slight difference in the underparts arose from 25% of the desert sample's being rated 2, paler than in any of the coastal specimens. Figure 19 is a scatterplot of these two groups showing the separation on the basis of wing length and rump/scapular color.

Two specimens of these groups were misclassified by the discriminant function. One is SDNHM 42931, the single February (comparatively worn and faded) coastal specimen, the other SDNHM 46003, an Imperial Valley specimen at the dark extreme for the species in rump/scapular color (rated 10), a color matched otherwise

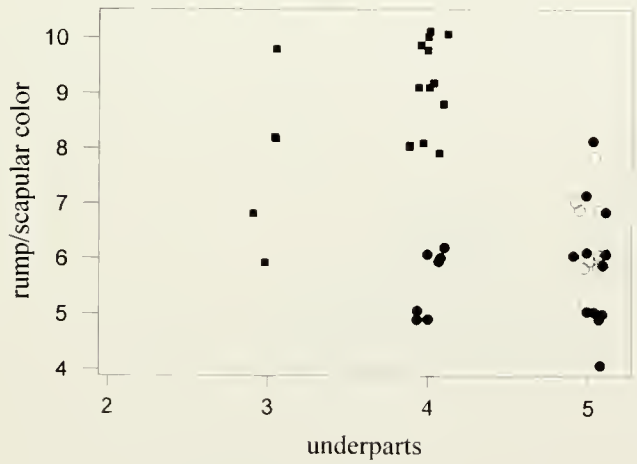

Figure 18. Scatterplot for *Cistothorus palustris aestuarinus* and coastal southern California Marsh Wrens of the pair of variables in which they differ most, rump/scapular color and underparts. ●, core (September) specimens from the San Joaquin Delta (*aestuarinus*); ○, additional (October) specimens from the San Joaquin Delta (inferred *aestuarinus*); ■, specimens of the breeding population of coastal southern California

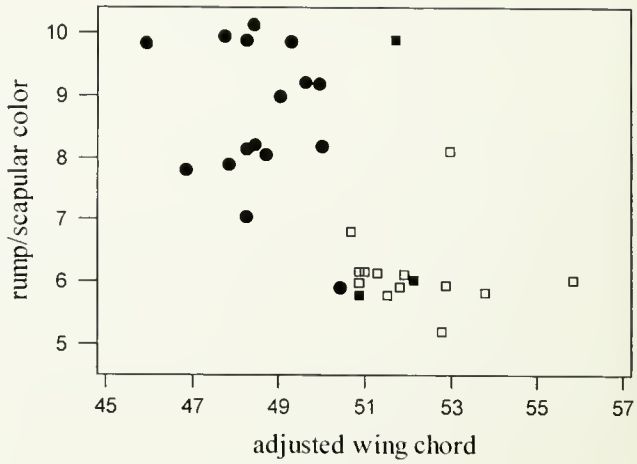

Figure 19. Scatterplot for *Cistothorus palustris deserticola* and coastal southern California Marsh Wrens of the two variables in which they differ most, wing length and rump/scapular color. So that the sexes could be considered together in one statistical process, the wing chords of females were multiplied by 1.06, the factor by which the average male Marsh Wren exceeds the average female. ■, core (August/September) specimens of the breeding population of the Colorado Desert (*deserticola*); □, additional October–February specimens from the Colorado Desert inferred as *deserticola* (see Figure 4); ●, specimens of the breeding population of coastal southern California.

only along the southern California coast. In wing length and crown pattern, however, this specimen is like *deserticola* and unlike the coastal sample.

The jackknife-corrected discriminant analysis suggested that only 5% of a sample of these two populations should overlap. Therefore, the name *deserticola* does not apply well to the southern coastal population.

ALLOCATION OF SPECIMENS FROM OTHER SITES

We applied the discriminant functions generated by both the core and enlarged samples to specimens from elsewhere in the Marsh Wren's breeding range.

Coos County, Oregon

Of two specimens collected 7.1 miles north of Coos Bay on 22 October 1982 (SDNHM 42077 and 44078), one was placed by the discriminant functions (from both the core and enlarged samples) with *deserticola*, the other with *aestuarinus*. That neither was placed with *paludicola* suggests that the southern limit of *paludicola* lies somewhere along the coast of central Oregon and does not reach California.

Humboldt County, California

A single immature male (SDNHM 3203), collected at Clam Beach on 18 October 1967, is older than the specimens on which the discriminant functions were based but we assessed it anyway, as it was still in heavy molt so presumably represents the local population. With a rump/scapular rating of 7 and a crown rating of 4, it is at the pale extreme for the southern California coastal population, but its short wings (apparently fully grown in at 48.8 mm) are typical of that group, to which the discriminant functions assigned it. With the exception of one specimen from the Imperial Valley, it is the only specimen from outside coastal southern California placed with that group.

Coastal Central California

Another somewhat aged specimen (SDNHM 35175), collected 18 September 1958 just northeast of Martinez in Contra Costa County, has paler underparts (rated 3) than the sample from just 10 miles to the northeast across Suisun Bay at Joice and Grizzly islands (all rated 4 or 5). Therefore, it matches *deserticola* better than *aestuarinus*, and that is where the discriminant functions placed it.

An old, foxed specimen (SDNHM 24642), collected 4 December 1938 at Santa Cruz, though not evaluated by the discriminant functions, appears closest to *deserticola* as well. The breast is only lightly tinged buff, while the crown is too brown and the wings too long (50.7/51.7 mm, female) for the southern coastal population.

A specimen from the mouth of Los Osos Creek on Morro Bay, San Luis Obispo County, collected 7 September 1986 (SDNHM 44461), was placed with *aestuarinus* by the discriminant function based on the core specimens alone, with *deserticola* by the function based on the enlarged sample. Of two specimens (SBMNH) from Dune Lakes, southwestern San Luis Obispo County (28 September 1962, 12 September 1973), the former was placed by the discriminant functions with *deserticola*, the latter with *aestuarinus*. Of two specimens from the Santa Ynez River mouth, Santa Barbara County (UCSB), one (4 January 1992) is clearly a migrant *plesius/pulverius*, while the other (10 January 1992) was placed by the discriminant functions with *aestuarinus*. Though the base for drawing a conclusion is rather meager, evidently the Marsh Wrens of coastal central California bridge the difference between *aestuarinus* and *deserticola*.

Oases of Mojave Desert

We examined specimens from two sites in the Mojave Desert, Harper Dry Lake, San Bernardino County, and Piute Ponds, Los Angeles County.

The specimens from the Piute Ponds, within Edwards Air Force Base in the Antelope Valley, are all in the Los Angeles County Museum. Five were collected on 27 October 1989. Of these, two are migrant *plesius/pulverius*, while the other three fit with *deserticola*. Six were collected in spring, from 26 April to 8 May. Three are juveniles; two are badly worn adults. One adult, a male with enlarged testes taken 26 April 1989, is still in a condition good enough to be assessed. It agrees well with *deserticola* in all variables.

From Harper Dry Lake, we assessed 17 specimens, all collected in fall and early winter, the earliest fall specimens being taken on 28 September. All were therefore taken at a time when migrants should be expected, and, not surprisingly, of the 17, 6 were identified by the discriminant functions as *plesius/pulverius*. Two additional specimens (SBCM), identified by the functions as *paludicola*, were probably migrants from the Great Basin as well. One had a rump/scapular score of 2, typical for *plesius/pulverius* but not for *paludicola*. With nape-collar widths of 5–6 mm, probably their necks were elongated in preparation in comparison to the specimens used in the defining samples, as they were made by different preparators. The other 9 Harper Dry Lake specimens are too dark on the rump, scapulars, and underparts for the migratory subspecies, so we infer these represent the resident population. Of the 9, 5 conform with *deserticola*, while 1 (SBCM 53683), with a nape-collar width of 5 mm and a back score of 2, was placed by the functions with *paludicola*. Again, this specimen may have had its neck overly stretched; in other variables it agrees with *deserticola*. Three specimens, by virtue of their darker underparts (especially striking in SDNHM 48952) or narrower back streaks, better fit *aestuarinus*. Though it is possible that these apparent *aestuarinus* dispersed southeast from the Central Valley, more likely they represent normal variation in the resident population. The dark extreme of underparts crops up in one specimen of *deserticola* from the Imperial Valley, and the narrower white back streaks (rated 2) in two specimens. As noted above, the distinction between *aestuarinus* and *deserticola* is comparatively weak, and despite the wide separation of the main ranges, the intervening oases may provide an opportunity for gene flow. Even in these nonmigratory subspecies, substantial dispersal ability likely favors survival of birds dependent on widely scattered tiny patches of suitable habitat.

Ventura County, California

Unfortunately, we located only a single recent specimen from Ventura County, a male taken at the sewage ponds in the Point Mugu military reservation on 13 December 1986 (SBMNH 5090). This specimen falls within the range of the southern coastal population in its fairly dark rump and scapulars (rated 7) and fairly blackish crown (rated 4) but disagrees in its long wings (53.4). The discriminant functions placed it with *deserticola*.

SUBSPECIES DEFINITIONS

These comparisons suggest that *plesius/pulverius*, *paludicola*, *aestuarinus*, and the population of coastal southern California are all differentiated at a level appropriate for designation as subspecies. *Cistothorus p. deserticola* presents a more awkward problem.

Cistothorus p. plesius/pulverius

Our analyses reaffirm the distinctiveness of the more or less migratory plateau population from the lowland populations nearer the Pacific Coast, a difference universally recognized since 1897. This group is identified by its comparatively long wing (a difference expected between migratory and sedentary populations), entirely brown to moderately black crown (Figure 20), narrow brown nape collar, broadly white-streaked back, comparatively pale tawny rump and scapulars, and pure white or only slightly buff-tinged breast (Figure 21). In combination these features sufficed to distinguish 92% of our sample.

Assessing the distinction between *plesius* and *pulverius* was not a goal of this study, and such an assessment was not possible from the sample used, which lacked specimens from the breeding range of *plesius*. The few specimens from eastern California were among the largest and palest of the sample, however, suggesting the Marsh Wrens breeding along the east side of the Sierra Nevada and Cascade Range (*pulverius*) represent the extreme development of this group's characters and may be distinguishable from the majority of winter visitors in southern California, in which these characters are on average less extreme and may be migrants from farther east in the Great Basin/intermountain region (*plesius*). The greater abundance of apparent *plesius* in winter in southern California, despite its breeding range's being more remote, may be due to a difference between *pulverius* and *plesius* in the winter climate of the breeding range. From the Pacific Ocean to the Rocky Mountains, winter temperatures tend to decrease from west to east, and wintering by Marsh Wrens in the ranges of *pulverius* and *plesius* has been reported as irregular and dependent on the severity of the winter (e.g., Root 1988; Gilligan et al. 1994).

Cistothorus p. paludicola

The sample from southwestern Washington stood apart from the others largely on the bases of its entirely brown to only slightly black-margined crown, broad brown nape collar, and narrowly white streaks on a reduced weakly black-tinged back patch. The rump/scapular ranking of *paludicola* overlapped extensively with those of *aestuarinus* and *deserticola* on our light-to-dark scale, but the hue of these parts of the plumage *paludicola* tends more toward an earth brown, and away from rufous, than in the other lowland subspecies, a subtle variation not captured in our analyses but evident in Figure 20. In wing length and underpart pattern *paludicola* occupies a position intermediate with and overlapping several other populations. The weakest separation of *paludicola* was from *aestuarinus*, but the darker underparts, blacker

Figure 20. Upperparts of six populations of the Marsh Wren. *Cistothorus palustris clarkae*, based on SDNHM 48915, holotype from Batiquitos Lagoon, Carlsbad, San Diego County, California, 23 August 1994. *C. p. deserticola* (best included under *aestuarinus*), based on SDNHM 44278, a topotype from 2 miles north-northwest of Seeley, Imperial County, California, 29 September 1985. *C. p. aestuarinus*, based on SDNHM 44532, virtual topotype from Joice Island, Solano County, California, 9 September 1986. *C. p. paludicola*, based on UW 40565, a topotype from the North River mouth, Willapa Bay, Pacific County, Washington, 18 November 1985. *C. p. plesius*, based on SDNHM 43971, from Picacho Reservoir, Pinal County, Arizona, 24 October 1985. *C. p. pulverius*, based on SDNHM 43469, from Owens Lake, 5 miles northeast of Olancha, Inyo County, California, 20 September 1984.

Figure 21. Underparts of six populations of the Marsh Wren, based on the same specimens as in Figure 20.

crown, narrower nape collar of the latter still served to allow 91% of that pair of populations to be distinguished.

Cistothorus p. aestuarinus

The Sacramento Delta sample differed from the other groups primarily on the basis of its dark underparts; the specimens ranked darkest (5) on the underparts were from this area almost exclusively. In wing length, rump/scapular color, crown pattern, nape-collar width, and back pattern the delta sample was in an intermediate position, as might be expected from its central position geographically. The extreme developments of some of the peripheral populations, however, *plesius/pulverius* in large size and plumage paleness, *paludicola* in its broad nape collar and brown crown, and the population of coastal southern California in its small size and dark upperparts, left *aestuarinus* adequately isolated from these. The distinction from *deserticola*, on the basis of darker underparts and narrower white back streaks alone, was the weakest but could be defined so that only 4 of 43 specimens from near the type localities in the combined enlarged samples overlapped with the other.

Cistothorus p. deserticola

Despite its peripheral position geographically, the population of the Colorado Desert is the least distinctive morphologically. In all characters, it lies in a position intermediate among the other subspecies. It differs from *plesius/pulverius* in its tendency toward a darker rump and scapulars, buffier underparts, shorter wings, and blacker crown. It differs from *paludicola* in its tendency toward darker rump and scapulars, a narrower nape collar, and bolder white back streaks. It differs from *aestuarinus* in its tendency toward paler underparts and narrower white back streaks. Its differs from the population of coastal southern California in its longer wings, tendency toward paler rump and scapulars and browner crown, and average slightly paler breast.

If only the type localities of *aestuarinus* and *deserticola* had to be considered, the two subspecies could be recognized fairly easily. But the samples from coastal central California and Harper Dry Lake show the whole range of these phenotypes. A distinction between the two implies a biogeographically oddly shaped zone of intergradation at least as large as the core ranges of the subspecies. Therefore, recognition of *deserticola* as distinct from *aestuarinus* does not seem practical, a result implied also by the group's failure to segregate in the cluster analysis.

The wide range (even to south-coastal Oregon) of Marsh Wrens matching the characters of *deserticola* suggests that the *deserticola* phenotype could represent the primitive appearance of California's lowland Marsh Wrens and that the dark underparts of *aestuarinus* are an innovation that arose in or near the San Joaquin Delta and has spread to some degree over most of California but has barely touched the southeastern corner of the state. Conversely, the *aestuarinus* type may have originally been widespread, and, especially before the damming of the Colorado River and irrigation of the Imperial Valley, *deserticola* was confined largely to the Colorado Delta. Changing water-management practices have probably increased the range and population of *deserticola* enormously in historic time (Rosenberg et al. 1991), possibly enabling it to invade northwest and mix with *aestuarinus*.

Southern California Coastal Population

The sample from San Diego County was well isolated from the others on the basis of having the shortest wing, most extensively black crown, and darkest rump and scapulars. In nape-collar width, back pattern, and underpart pattern it did not differ greatly from several other samples, overlapping in those features substantially. But the sample stands at the extreme for the species in three of the six characters quantified in this study. Cluster and discriminant analyses consistently identified it as an independent group. In all discriminant analyses, both pooled and pairwise, 91% or more of this sample was classified as expected on the basis of origin, while no more than 6% of any other sample was classified with the San Diego group, even when the discriminant functions were cross-validated via jackknifing. Because the level of differentiation of this sample well exceeds the 75% threshold, and equals or exceeds that of other subspecies recognized in the Marsh Wren, we propose that it be known as

Cistothorus palustris clarkae subsp. nov.

Holotype. San Diego Natural History Museum number 48915, collected by Philip Unitt (original number 1357) on 23 August 1994 at the east end of Batiquitos Lagoon, city of Carlsbad, San Diego County, California (35° 06′ N, 117° 16′ W). Adult female (skull completely pneumatized; ovary granular, 4 × 1.5 mm; ova minute). Weight 8.1 grams; slight fat. Length in flesh 123 mm, wingspread 156 mm, wing chords 47.1 mm. Prebasic molt completed except for a few feathers on chin and face.

Diagnosis. Differs from other western populations of the Marsh Wren in small size (see Table 3), more extensively black crown (at least 50% black; usually with only a small brown patch in the center of the forehead), and darker rufous scapulars, rump, upper tail coverts, and central rectrices, in fresh plumage all of these close to Raw Umber or Prout's Brown of Smithe (1975).

The new subspecies differs from *deserticola*, as suggested by jackknife-adjusted discriminant analysis, at a 94% level (at least) by these three characters, plus a slight tendency to a darker breast. A single exceptionally dark specimen of *deserticola* and a probably faded February specimen of *clarkae* were the only two confounding specimens. In the sample examined wing length alone yielded 100% separation.

From *aestuarinus*, *clarkae* differs at a nearly 100% level by its usually darker rump and scapulars, shorter wing, paler underparts and flanks (breast pale buff), and blacker crown. In combination these characters distinguish 100% of specimens from the type locality. From the broader range of *aestuarinus*, as we redefine it, including all of coastal California south to Ventura County and the Mojave and Colorado deserts (*deserticola*), only 2 of 60 specimens (3%) were placed by the discriminant functions with *clarkae*.

From *paludicola*, with which it has traditionally been linked, *clarkae* differs at a 100% level by its bolder white back streaks on a blacker background, and narrower brown nape collar (2–7 mm in *clarkae*, >5 in only 2 of 23 specimens; 4–9 in *paludicola*, <5 in only 3 of 20 specimens) in addition to the three other characters.

From the migratory plateau subspecies *pulverius* and *plesius*, which invade its range in fall and winter, *clarkae* differs even more in the three main characters than it does from the other lowland populations, plus it has a more intensively buff breast. From the Marsh Wrens of northeastern North America (*laingi*, *iliacus*, *dissaeptus*, and nominate *palustris*), *clarkae* differs in its barred upper tail coverts as well as its darker rump and scapulars and buff breast band. From the Marsh Wrens of the coastal southeastern United States *clarkae* differs as follows: from *thryophilus* by its largely blackish crown, from *marianae* and *waynei* by its more rufous rump and scapulars and lack of dusky speckling or barring on the flanks or breast, and from *griseus* by its far more rufous rump and scapulars and more extensive black and white patch on the back. From *tolucensis* of central Mexico *clarkae* differs by its less extensive black and white back patch and paler, less rusty underparts.

Distribution. Coastal lowland of southern California, from the Tijuana River immediately north of the Mexican border north to Los Angeles. Of 25 old October–February Marsh Wrens from Los Angeles and Orange counties in the Los Angeles County Museum of Natural History, 22 appear to be migrants of *plesius/pulverius*, while

TABLE 3. Wing chords of various subspecies of the Marsh Wren.

	n	Mean	Range	Standard Deviation
Males				
C. p. plesius/ pulverius	11	54.9	51.0–57.1	1.93
C. p. paludicola	16	51.3	49.5–52.4	0.70
C. p. aestuarinus	15	51.4	49.5–53.3	0.97
C. p. deserticola	5	52.4	51.7–53.8	0.81
C. p. clarkae	12	48.2	44.0–50.4	1.84
Females				
C. p. plesius/ pulverius	13	50.3	48.2–52.2	1.16
C. p. paludicola	4	46.4	45.3–48.2	1.09
C. p. aestuarinus	12	48.0	46.5–51.3	1.36
C. p. deserticola	11	49.0	47.8–52.7	1.39
C. p. clarkae	12	45.6	43.3–47.1	1.09

3 agree with *clarkae* in their extensively black crowns (rated 5 or 6), dark (now foxed and unscorable) rump and scapulars, and short wings (46.2 in the one female; 44.7 and 48.2 in the two males). These are LACM 12289, from the San Gabriel River on 23 December 1895, LACM 2376, from Nigger Slough on 12 February 1918, and LACM 17629, from Playa del Rey on 20 December 1931. These specimens demonstrate that the characters of *clarkae* are long established in this population, not an artifact or innovation of the recent sample from San Diego County.

The breeding Marsh Wrens of western Riverside County probably belong with *clarkae*, though this needs confirmation with recent specimens. The only specimen we have seen from this area, SBCM 3912, is a migrant *plesius* collected 12 March 1967. For further details and historical changes, see below.

One specimen implies short-distance dispersal of *clarkae* across unsuitable habitat. This is LACM 19635, a male collected by George Willett on 13 November 1939 on San Clemente Island, where the Marsh Wren is only a rare nonbreeding visitor (Jorgensen and Ferguson 1984). The rump is as dark as in the three old specimens of *clarkae* from Los Angeles County. The crown seems to have lost a few feathers so is difficult to judge but looks about half black. At only 48.0 mm, the wing measurement is typical of *clarkae*.

Etymology. We name this Marsh Wren in honor of Mary Hollis Clark, in appreciation of her 33 years of support and service, through good times and bad, to the San Diego Natural History Museum and its scientific and educational mission. With the help of Mrs. Clark and her family, many San Diegans have increased their appreciation of the uniqueness of their natural environment. With its narrowly restricted range, *Cistothorus palustris clarkae* reveals itself as yet another element of that uniqueness.

Discussion. Our results confirm Rea's (1986) conjecture that the coastal southern California Marsh Wrens constitute a subspecies, though not quite on the basis that he suggested. As noted above, the pigment coloring the rump and scapulars of Marsh Wrens is subject to foxing, increasing its redness. Evidently, the greater the concentration of this pigment, the more grossly the specimen foxes. In the pale extreme of the species (*pulverius*) the difference is slight; in the dark extreme (*clarkae*) the difference is great, as seen in comparison of our 1994 specimens with the three collected in Los Angeles County from 1895 to 1931. The rump and scapulars of old specimens, in which the natural darkness of *clarkae* has been foxed into rustiness, look "brighter and richer" (Rea 1986) than in the other subspecies.

Swarth (1917) noticed that the Marsh Wrens of coastal southern California were exceptionally small but did not quantify the difference. Neither he nor subsequent revisers applied this variable to the population. The difference in crown pattern has not been reported previously.

Revelation of an undescribed subspecies of bird in a region as heavily populated as coastal southern California, which has been studied by thousands of biologists, may seem incongruous. In the case of *Cistothorus palustris clarkae*, however, several factors contributed toward concealing it for so long. In existing collections, the great majority of specimens of the Marsh Wren from coastal southern California were taken in winter, and consist largely of migrants from the plateau region. Since there is substantial variation among these migrants, probably interpretable as two subspecies, the additional variation arising from the few specimens of *clarkae* was less noticeable. Some individuals of *paludicola* and *aestuarinus* were thought to make long-distance migrations, reaching coastal southern California, for which we have seen no evidence. The few breeding-season specimens (e.g., SBCM 36797, Nigger Slough, Los Angeles County, 13 May 1917) are in poor condition, often with worn crowns, faded rumps and scapulars, and broken primary tips; they do not preserve well the defining features of *clarkae* evident in fresh plumage. The very urbanization of the range of *clarkae* discourages collectors from working in it; collecting birds at most sites in coastal southern California where Marsh Wrens breed now requires special authorizations beyond the standard permit from the California Department of Fish and Game.

DISTRIBUTIONS OF THE SUBSPECIES OF THE MARSH WREN IN SOUTHERN CALIFORNIA

Cistothorus p. plesius/pulverius

Marsh Wrens from the Great Basin/intermountain plateau region winter throughout southern California, invading many areas where the species does not breed. Though Garrett and Dunn (1981) reported the Marsh Wren as absent from the "colder northern deserts" in winter, T. Heindel (pers. comm.) finds it more common in the Owens Valley in winter than in summer. West of the Sierra Nevada, Grinnell and Miller (1944) reported *plesius* north only to Tomales Point and Petaluma, Marin and Sonoma counties. Gabrielson and Jewett (1940) did not report it from west of the Cascade Range in Oregon, but in Jewett's collection (SDNHM) are three specimens, from Taft, Netarts, and Portland, that conform with the interior population well in both color and size. The specimen from Portland (6 October 1928, SDNHM 24646, wings 55.5/56.0 mm) apparently represents the northwesternmost documented point of these migrants' dispersal.

Understanding of the schedule of arrival and departure of *plesius/pulverius* in southern California needs further refinement. We have not seen any specimen earlier than one taken for this study in the Tijuana River valley, San Diego County, on 23 September 1994 (SDNHM 48983). But the migration unquestionably begins somewhat earlier than this; M. Heindel (pers. comm.) finds Marsh Wrens migrating commonly through the desert oases of eastern Kern County by 10–20 September; M. A. Patten (pers. comm.) has earliest dates for migrants in the California deserts of 11 and 17 September; Lehman (1994) reported migrants as fairly common in Santa Barbara County by the beginning of September. Marsh Wrens have been reported away from breeding sites as early as 29 August in eastern Kern County (M. Heindel pers. comm.), 14 August in San Diego County (Unitt 1984), and 23 July in Santa Barbara County (Lehman 1994). We suspect the few early records represent short-distance dispersal from breeding sites nearby and that migrants from the plateau region do not reach the coast of southern California until around the middle of September. But the exact schedule and possible annual variations of this arrival remain uncertain, requiring testing via further collecting.

Spring departure takes place largely in April. We have not seen specimens of *plesius/pulverius* from the winter range later than 13 April (1923, salt marsh at Santa Catarina Landing, 29° 30′ N, Baja

Figure 22. Distribution of the Marsh Wren as a breeding species in southern California. Squares, *Cistothorus palustris pulverius*; circles, *C. p. aestuarinus* (including *deserticola*); upright triangles, recent sites for *C. p. clarkae*; inverted triangles, former sites for *C. p. clarkae*. Filled symbols, specimens examined; open symbols, other sites where the Marsh Wren is known to have bred or summers regularly (subspecies allocation inferred at these sites). These sites are based on published literature, personal observation, personal communication from many field ornithologists, and the egg collections of the Western Foundation for Vertebrate Zoology, Camarillo, and the San Bernardino County Museum, Redlands.

California, SDNHM 8626) and 16 April (1920, Furnace Creek Ranch, Death Valley, Inyo County, MVZ 40664), but Marsh Wrens continue to be seen in dwindling numbers at nonbreeding sites in southern California nearly or quite to the end of the month. In the Mojave Desert of eastern Kern County, sightings as late as 15 May are known but exceptional (M. Heindel pers. comm.). Records later in the spring (4 June, Galileo Hill, Kern County, M. Heindel pers. comm.; 8 June, Southeast Farallon Island, Pyle and Henderson 1991) may represent vagrants of far distant subspecies; specimens are needed to test this.

Grinnell and Miller (1944) showed the Marsh Wren as absent as a breeding species from Inyo County, but summering birds are currently widespread and common along the entire Owens River, south to Owens Lake (T. Heindel pers. comm.) (Figure 22). They occur also at Little Lake. More specimens are needed to confirm this population as *pulverius*, but a specimen from Owens Lake, collected on 20 September 1984 (SDNHM 43469), we believe represents that population, even though migrants from farther north might be expected on that date. It was not fat and was still molting its contour feathers; it is at the extreme for *pulverius* in paleness of crown, scapulars, rump, and underparts, being scored at 1 in those variables. Therefore, we suggest the breeding range of *pulverius* extends south in California to Owens Lake and probably to Little Lake, in southwestern Inyo County.

In eastern Inyo County, the Marsh Wren is known to nest at Furnace Creek Ranch, Death Valley (T. Heindel, M. A. Patten pers. comm.) and presumed to along the Amargosa River near Tecopa (regular through the summer, J. Tarble pers. comm.). But the only specimen we have seen from these sites (Furnace Creek Ranch, 16 April 1920, MVZ 40664), is a late migrant. Though the testes are somewhat enlarged (about 4 mm long, according to the drawing on the label), the bird was fat and not in breeding habitat ("rank grass and mesquite at edge of alfalfa," according to the field notes of the collector, Joseph Grinnell). In paleness of rump and scapulars, whiteness of rump, boldness of white back streaks, and large size (wing chord 54.5 mm), it is clearly *plesius/pulverius* and matches May specimens of *pulverius* from southeastern Oregon. The occurrence of a typically low-desert riparian avifauna at Furnace Creek Ranch and Tecopa suggests the Marsh Wrens nesting there are more likely *aestuarinus/deserticola*.

Cistothorus p. paludicola

We found no specimens suggesting this subspecies occurs in California. Since the discriminant analysis did not place even the two specimens from Coos County, Oregon, with *paludicola*, we infer it does not reach California as a breeding species. The southernmost specimen we have seen is from Taft, Lincoln Co., Oregon (5 January 1935, SDNHM 24647). Though the possibility remains that *paludicola* migrates to some extent to northern California, we doubt this and suggest that *paludicola* be deleted from the list of California birds unless further studies confirm it.

Cistothorus p. aestuarinus

The pattern of variation in the Marsh Wren in California seems best described by including all the populations of the north and central coast, Central Valley, and Mojave and Colorado deserts in this subspecies.

From northern Monterey County, where Marsh Wrens nest around Monterey Bay and in the lower Salinas Valley (R. F. Tintle in Roberson and Tenney 1993), the species is absent along the coast south to Morro Bay, San Luis Obispo County. Another population breeds in coastal marshes from Morro Bay to the Santa Ynez River mouth (Lehman 1994).

Then another gap intervenes until another isolated population occupies part of Ventura County. In Ventura County Marsh Wrens nest near the Santa Clara River at the duck ponds 5 km east of Santa Paula (Z. Labinger pers. comm.). More intensive study may reveal them elsewhere along the Santa Clara River, but the population if any is not large or continuous (M. A. Holmgren pers. comm.). Marsh Wrens also breed in diked ponds of the Ventura County Gun Club, just northwest of Mugu Lagoon (D. DesJardins pers. comm.), and in at least one location around Mugu Lagoon itself, on the grounds of the Pacific Missile Test Center (T. W. Keeney pers. comm.).

The single specimen we saw that apparently represents the breeding population of Ventura County has a rump and crown at the pale extreme for *clarkae* and a wing longer than in specimens from Los Angeles to San Diego. It is closer to *deserticola*. Ventura County may represent an area of intergradation between the two, or the characters of *clarkae* may have arisen only from Los Angeles south. One might expect that the original range of *clarkae* resembled that of the Light-footed Clapper Rail, *Rallus longirostris levipes*, or Belding's Savannah Sparrow, *Ammodramus sandwichensis beldingi*, both of which reached their northern limits at Santa Barbara, but the Marsh Wren, with its freshwater ecology, may be responding to different selective forces.

In the Mojave Desert, the Marsh Wren occurs through the summer at several oases. In eastern Kern County, Matt Heindel (pers. comm.) has confirmed its nesting at three sites: the South Base sewage ponds on Edwards Air Force Base, near Cantil (about two territories only), and at China Lake. Also, Marsh Wrens have summered and probably have nested at California City; regular clearing of marsh vegetation hinders the birds from establishing themselves there. The marshes at all of these sites are supported by artificially developed water sources, so the Marsh Wren's breeding in eastern Kern County must represent rather recent colonization.

In the Antelope Valley of northern Los Angeles County, the Marsh Wren breeds abundantly at one known site, the Piute Ponds 10 km north-northeast of Lancaster (specimens of both juveniles and breeding adults in LACM).

In San Bernardino County, nesting has been confirmed at Saratoga Springs at the south end of Death Valley (Austin 1970), Mojave Narrows Regional Park along the Mojave River, (S. J. Myers pers. comm.), Harper Dry Lake (E. A. Cardiff pers. comm.), and (irregularly) at Morongo Valley. Nesting is possible at Barstow (sewage ponds), Twentynine Palms, Afton Canyon, Zzyzx Spring, and Camp Cady (E. A. Cardiff, S. J. Myers, M. A. Patten pers. comm.)

Breeding Marsh Wrens remain locally common the length of the Colorado River in California, in the Imperial Valley, and around the Salton Sea, the area assigned by Rea (1986) to *deserticola*.

Cistothorus p. clarkae

The range of *clarkae* is confined to coastal southern California from Los Angeles south, and even within this region is patchy, owing to the natural localization of freshwater and brackish marshes in this arid region and the extensive destruction of wetlands over the past century. Yet in San Diego County the subspecies is widespread and has apparently extended its range or at least increased in numbers over the past 25 years. The southernmost site is the Tijuana River Valley immediately north of the Mexican border, where Marsh Wrens colonized borrow pits along Dairy Mart Road, beginning in 1980 as the ponds' marshes matured, and becoming common by the late 1980s. Breeding Marsh Wrens have never been reported along the Pacific coast of Baja California (Grinnell 1928, Wilbur 1987); Kurt Radamaker (pers. comm.) confirms their absence at the northernmost sites with possibly suitable habitat, Descanso and La Misión; neither has he found them in the inland freshwater marshes near Ojos Negros.

The next known site to the north is Mission Valley, along the San Diego River in the city of San Diego. Marsh Wrens are not known to have nested there before 1978, though the San Bernardino County Museum has a set of eggs taken at "San Diego" in 1953 (Unitt 1984). The vegetation along 2.3 km of the San Diego River was removed in 1988 and 1989, as part of a flood-control scheme. Marsh vegetation began regrowing along the recontoured river banks immediately. Unitt surveyed the site regularly for birds, as part of monitoring a revegetation program, and found that Marsh Wrens recolonized the area in the summer of 1993.

The population along Santa Ysabel Creek from Lake Hodges to San Pasqual in central San Diego County, first noted in 1978 by Kenneth L. Weaver, is clearly a recent colonization, since the area was a center of activity for early twentieth-century egg collectors (Unitt 1984). Sharp (1907) specifically denied the Marsh Wren's occurrence at San Pasqual.

In central and northern San Diego County, from Los Peñasquitos Lagoon north, Marsh Wrens are resident in every coastal wetland supporting stands of bulrushes and cattails. Along the San Luis Rey river, they extend inland at least to 2.4 miles northeast of Bonsall (male with enlarged testes on 28 February 1984, SDNHM 42931); along the Santa Margarita River, to O'Neill Lake (20 on 28 June 1995, Unitt pers. obs.). From published literature and the egg collection at the Western Foundation of Vertebrate Zoology, Guajome Lake is the only site in San Diego County where the Marsh Wren was confirmed nesting before 1949; the "San Luis Rey" of Sharp (1907) may encompass the river's lower floodplain, including Guajome Lake.

In Orange County, Marsh Wrens are abundant through the breeding season at Upper Newport Bay and the San Joaquin Marsh 3 km to the northeast in Irvine. Elsewhere in this county, however, they are far less common and less well known. They are resident at the Bolsa Chica wetlands in the city of Huntington Beach and at Seal Beach National Wildlife Refuge, but in what numbers is unclear. Farther inland in Orange County, there are no large marshes suitable for Marsh Wrens. The one known (small) population is in restored habitat along the Santa Ana River in Anaheim, which the wrens colonized in the late 1980s. The species may occupy other sites ephemerally, as in Huntington Central Park, city of Huntington Beach (D. R. Willick, R. A. Hamilton pers. comm.)

In coastal Los Angeles County, breeding Marsh Wrens are now restricted to Alamitos Bay, Long Beach, and Harbor Lake, in the Harbor City district of Los Angeles (K. L. Garrett pers. comm.) These sites are the last remnants of marshes extensive before the development of the Los Angeles and Long Beach harbors. Marsh Wrens nested widely in the Los Angeles Basin before urbanization, and this area likely represented the core of the range of *C. p. clarkae*.

In western Riverside County, Marsh Wrens remain common all year in Prado Flood Control Basin along the Santa Ana River (J. Pike pers. comm.) and occur locally along the river between Prado Basin and the city of Riverside (at least at Hidden Valley Wildlife Area at the western edge of the city of Riverside. M. A. Patten pers. comm.). Elsewhere in western Riverside County, Marsh Wrens summer along Alberhill Creek where it enters Lake Elsinore (M. A. Patten pers. comm.) and at San Jacinto State Wildlife Area near Lakeview (A. M.

Craig, R. McKernan pers. comm.). Other unreported colonies in this area are possible. Specimens from this area are needed to test whether this population represents *clarkae*, *aestuarinus/deserticola*, or intergrades. Though the area is closer to the range of *clarkae* than to that of *aestuarinus/deserticola*, quite possibly *clarkae* is confined to a narrow coastal strip.

With urbanization, *C. p. clarkae* evidently lost much of its original core range in Los Angeles and Orange counties. Yet it appears to have spread its range southward in San Diego County rather recently, a seeming contradiction. Environmental change, however, may favor as well as eliminate the Marsh Wren in some cases. Man-made lakes are quickly colonized by marsh plants, creating new Marsh Wren habitat. Urbanization of the coastal lowland increases runoff, which in turn increases the rate of siltation of coastal lagoons. With the flushing force of their tidal prism reduced by siltation, and typically reduced further with several levees serving as roadbeds, the lagoons frequently have their mouths blocked with sand and cobbles. Fresh water from the increased runoff replaces the salt water from the tides, and freshwater marsh vegetation suitable for nesting Marsh Wrens replaces saltmarsh vegetation that isn't. We suspect these processes are largely responsible for increasing the population of *C. p. clarkae* in San Diego County. Efforts at some lagoons (including the type locality of *C. p. clarkae*) to reinstitute tidal flushing may reverse this trend locally, but the forces driving it will probably continue to sustain a healthy population of Marsh Wrens unless complete elimination of coastal wetlands resumes. For an accurate assessment of the subspecies' abundance, however, a rangewide survey is desirable.

ACKNOWLEDGMENTS

We thank Bert and Margaret McIntosh, Scott Tremor, and Lucie W. Clark for their indispensable help in the field, with handling the mist nets. We thank Robert R. Copper and the San Diego County Parks Department for special authorization to mist-net at San Elijo Lagoon and in the Tijuana River valley. Michael A. Patten helped with preliminary statistical analysis and offered many useful suggestions throughout the study. Ned K. Johnson, Mark A. Holmgren, Paul W. Collins, Robert McKernan, and Kimball L. Garrett graciously lent specimens from the University of California, Berkeley, University of California, Santa Barbara, the Santa Barbara County Museum of Natural History, the San Bernardino County Museum, and Los Angeles County Museum of Natural History, respectively. Clark Sumida kindly sent copies of the egg-collection records from southern California in the Western Foundation of Vertebrate Zoology, Camarillo. Many people graciously supplied details on the Marsh Wren's current distribution in southern California; for this we thank Kurt F. Campbell, Eugene A. Cardiff, Alan M. Craig, Don DesJardins, Kimball Garrett, Robert A. Hamilton, Tom and Jo Heindel, Matt Heindel, Mark A. Holmgren, Thomas W. Keeney, Zev Labinger, Robert McKernan, Michael A. Patten, Jim Pike, Kurt Radamaker, Jan Tarble, and Douglas R. Willick. We are enormously grateful to Nicole Perretta for lending us her artistic talent with the exquisite paintings featured in Figures 20 and 21. We thank Robert W. Dickerman, Robert A. Hamilton, Kimball L. Garrett, Mark A. Holmgren, and Kenneth C. Parkes for their constructive reviews. And we especially thank Amadeo M. Rea for providing the initial direction and opportunity to pursue this study.

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